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The Role of the "Third Eye" in Reptilian Behavior

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INTRODUCTION

The pineal gland remains an organ of uncertain function despite extensive research (see summaries of literature: Pflugfelder, 1957; Kitay and Altschule, 1954; and Engel and Bergmann, 1952). Its study by means of pinealectomy has been hampered in the higher vertebrates by its recessed location and association with large blood vessels which have made difficult its removal without brain injury or serious hemorrhage. Lack of purified, standardized extracts, improper or inadequate extraction techniques (Quay, 1956b), and lack of suitable assay methods to test biological activity have hindered the physiological approach. It seems probable that the activity of the gland varies among different species (Engel and Bergmann, 1952), between individuals of the same species, and within the same individual. This may also have contributed to the variable results obtained with pinealectomy, injection, and implantation experiments.

The morphology of the pineal apparatus is discussed in detail by Tilney and Warren (1919) and Gladstone and Wakely (1940). Only a brief survey is presented here for orientation. In living vertebrates the pineal system in its most complete form may be regarded as consisting of a series of outgrowths situated above the third ventricle in the roof of the diencephalon. In sequence these outgrowths are the paraphysis, dorsal sac, parapineal, and pineal bodies. The paraphysis, the most

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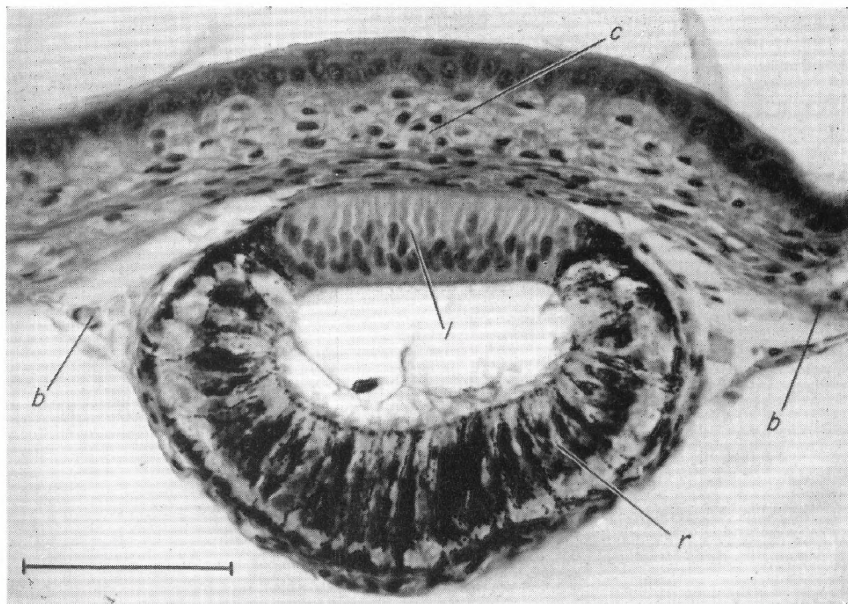


FIG. 1. Cross section of the parietal eye of *Sceloporus occidentalis*. The cornea and lens are transparent in life. Note the melanic pigment associated with the rod-like cells of the retina. The reticulum in the chamber of the "eye" is presumed to be coagulated secretion produced by the retinal cells. The diameter of the "eye" may be 0.25 mm. in a lizard 70 mm. in snout to vent length. *Abbreviations:* b, blood vessels; c, cornea; l, lens; r, retina. Horizontal line represents 0.1 mm.

anterior structure, is vascular and may develop villi that extend into the third ventricle. The dorsal sac may be a smooth, thin-walled structure or may also become invaginated and vascularized. In lampreys (*Petromyzon* and *Geotria*) there are two median, eye-like structures. The larger one, with well-differentiated lens and retina and socketed in the roof of the skull, has been called the parietal organ (or pineal eye) and the smaller one the parapineal organ (Studnicka, 1905). The median "eyes" of lampreys may represent an original pair of pineal structures that existed in ancient vertebrates, a view recently supported by studies of Edinger (1956) on Devonian fishes. In other vertebrates, however, the two elements (parapineal and pineal) are said to display varied development. One element or the other may produce an end vesicle—the pineal element in tadpoles and some frogs (Stieda's organ), the parapineal in *Sphenodon* and lizards (the parietal eye)—or the parapineal may be lacking altogether (fishes, birds, and mammals).

Actually, at the present time, there is uncertainty as to whether the

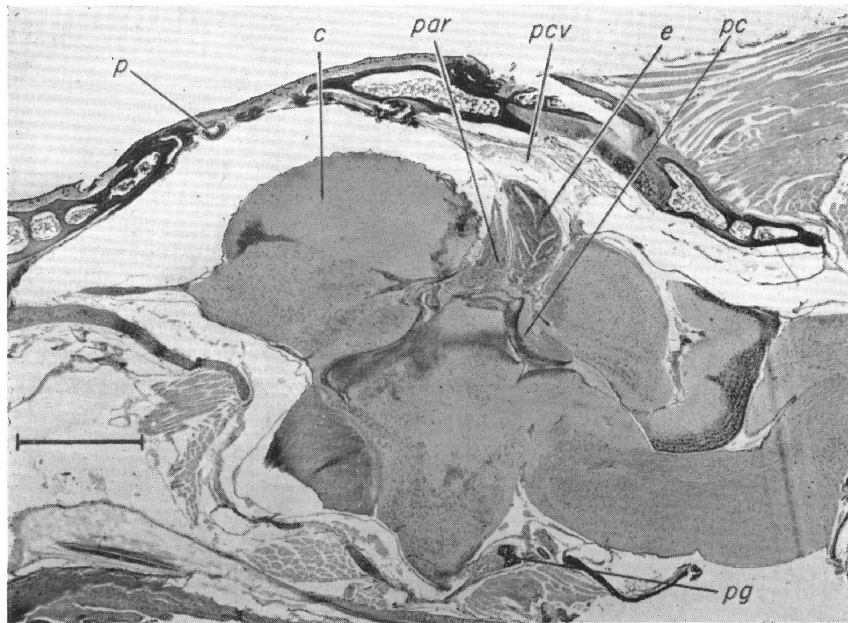


FIG. 2. Median sagittal section through the brain of *Sceloporus occidentalis*, showing the relative positions of the parietal eye and epiphysis. The length of the epiphysis may be 2 mm. in a lizard 70 mm. in snout to vent length. Abbreviations: c, cerebrum; e, epiphysis; p, parietal eye; par, paraphysis; pc, posterior commissure; pcv, sinus of posterior cerebral vein; pg, pituitary gland. Horizontal line represents 1 mm.

parapineal eye of lampreys is homologous with the parietal eye of lizards or not. The embryological studies of Steyn (1957) indicate that the parietal eye in some lizards develops anteriorly in the same out-pocketing that gives rise to the pineal gland. There is no clear indication that a separate (parapineal) element is involved. Perhaps an earlier stage involving separate anlagen is slurred over.

Cranial impressions and pineal foramina in fossil forms indicate that pineal structures existed in the early vertebrates. The presence of the pineal foramen in ostracoderms, primitive fishes, amphibians, and reptiles suggests widespread occurrence of a "third eye" (or perhaps a pair of "eyes" in Devonian fishes) in the cranial roof. Among many ancient reptiles the parietal foramen was much larger in relation to the size of the brain than in any extant form (Edinger, 1955). In some reptiles cranial recesses also indicate the presence of an epiphysis of large size (Camp, 1942).

A survey of comparative histology and morphology of the pineal system leads to the following generalizations:

1. Pineal structures are widespread throughout the vertebrates and constitute one of the oldest parts of the vertebrate brain.

2. In many species, particularly among the cold-blooded animals, the pineal apparatus is in a position to be acted upon by solar radiation. When an end vesicle is present, it is located under a layer of translucent skin (tadpoles and some frogs) or in or beneath a light-transmitting region of the skull, usually in a foramen covered by transparent skin. The end vesicle may (lampreys, some amphibians, *Sphenodon*, and some lizards) or may not (many lizards) have a nerve connection with the brain. In the absence of an eye-like organ, the pineal organ itself may lie beneath the translucent region (fishes). In some birds and mammals, although no specialized area of translucency is present, the gland lies immediately beneath the skull and is connected to the brain by means of an elongate stalk (rabbits, mice, and some birds).

3. The pineal organ or epiphysis¹ appears to be glandular in most vertebrates and has been shown to be secretory in the fish *Astyanax mexicanus* (Lowenstein, 1956).

4. When a parietal eye nerve is present, it connects with the habenular apparatus. At least this seems to be the situation in the following forms: *Sphenodon* (Dendy, 1911), *Iguana* (Strahl and Martin, 1888, and Klinckowström, 1893) and *Anguis* (Studnicka, 1905). In mammals and probably also in reptiles, the habenular ganglia are connected with the hypothalamus and midbrain by means of the striae medullaris thalami and the habenulo-peduncular tract. In elasmobranch and teleostean fishes, amphibians, reptiles (lizards and snakes), and mammals, a pineal nerve may connect the pineal organ with the posterior commissure (Gladstone and Wakely, 1940, p. 408), and in some species connections are established also with the internal capsule, striae medullares thalami, Meynert's bundles, habenular commissure, and optic tracts (Darkschewitsch, 1886).

5. The pineal body is usually closely associated with the vascular paraphysis and dorsal sac and may be itself highly vascular. In experiments with mammals, use of vital stains indicates that there is no impediment to diffusion between the blood and the gland such as exists between blood and brain parenchyma. In reptiles the posterior cerebral vein may be sinus-like and is closely associated with the epiphysis.

Anatomical evidence reveals marked phyletic constancy. The epiphysis has persisted despite the enlargement of the corpus callosum that

¹ We treat the terms "epiphysis" and "pineal organ" as synonyms.

has accompanied expansion of the cerebral hemispheres with advancing mental development. The close association with important neural pathways, the abundant blood supply, and cytological evidence (Quay, 1956a, 1956b; Oksche, 1956) suggest a high level of physiologic activity of the epiphysis. Specializations for light reception in cold-blooded vertebrates suggest a sensory role with respect to solar radiation.

We cannot review here the extensive physiologic literature. The summaries mentioned will bring the reader nearly up to date. Additional contributions are referred to below. Several points emerge as particularly noteworthy with respect to function. Among mammals a high level of metabolic activity is indicated by the marked capacity of the pineal to take up radioactive phosphorus and iodine. Phosphorus uptake by the pineal in the rat, guinea pig, rabbit, pig, and cat is three times that of the pituitary and 20 times that of the cerebellum (Borell and Örström, 1945, 1947), and in the rat its uptake of iodine was found to be greater than that of any organ other than the thyroid (Reiss *et al.*, 1949). Experiments, chiefly on birds and mammals, indicate an effect on the reproductive system (see Kitay and Altschule, 1954; Thiéblot and Le Bars, 1955). In lampreys (Knowles, 1939; Young, 1935), fishes (Breder and Rasquin, 1950), and amphibians (McCord and Allen, 1917) there is an influence on melanic pigment dispersal and response to light. Studies on reptiles suggest a role in metabolism (Clausen and Mofshin, 1939) and reproduction (Clausen and Poris, 1937).

One of the difficulties in pineal experimentation with the usual laboratory animals (rats, rabbits, chickens) has been poor survival following surgery. This has been due chiefly to hemorrhage and brain damage. There has also been the usual uncertainty as to what the findings may mean in relation to animals living in the wild. There appears to have been no previous attempt to test the importance of pineal structures in the survival of wild animals. Hence, in addition to the laboratory approach, we have selected for study a species that would lend itself well to field study. It was our hope that surgically treated wild animals would provide clues to pineal function that heretofore had been obscure in laboratory tests.

Among living reptiles, *Sphenodon* and many species of lizards have both a pineal organ (epiphysis; fig. 2), apparently homologous with that of fishes, birds, and mammals, and an eye-like parapineal (?) organ, the parietal eye (figs. 1, 2). A discrete end vesicle has been found elsewhere among adult extant vertebrates only¹ in lampreys and salientians. Thus

¹ In swan embryos (Krabbe, 1955) the swelled distal end of the epiphysis, and in the embryos of certain mammals (Krabbe, 1929) a small globular formation associ-

in lizards, animals that can be readily studied in the field, two fundamental parts of the pineal system are present. As descendants of animals (extinct reptiles) that gave rise to the birds and mammals, the study of lizards may be expected to shed light on the function of the pineal gland in higher vertebrates.

MATERIALS AND METHODS

The western fence lizard (*Sceloporus occidentalis*), a common species in the vicinity of Berkeley, California, has been our chief subject of study. Information is available on its population behavior (Fitch, 1940) and Stebbins (Stebbins and Robinson, 1946) had studied population dynamics in a closely related form, *Sceloporus graciosus*. It was expected that this background would facilitate detection of deviations from normal behavior should they occur in the field animals subjected to parietal-eye or pineal extirpation.

The fence lizard is hardy in captivity, and there have been no deaths attributable to pineal surgery. In the removal of the superficially located parietal eye (parietalectomy) no anesthesia is required. The epiphysis can be removed under cold anesthesia (the lizard buried in cracked ice) from which the animal promptly recovers. Results of experiments on the epiphysis will be reported in a subsequent paper.

Following removal of the outer layer (stratum corneum) of the interparietal scale, the parietal eye is exposed by reflexing the anterior part of the scale. The "eye" can be destroyed without removing its connective tissue capsule or entering the cranial cavity. The scale, including the stratum corneum, is returned to its former position. The same surgery is performed in the control animals, but the eye is left intact (fig. 3). Such animals are referred to below as "sham-operated." Collodion is used to seal the margins of the interparietal scale.

FIELD STUDY OF PARIETALECTOMIZED LIZARDS

The area chosen for the field study, in which both senior and junior author participated, was at an elevation of from 1300 to 1500 feet on the south-facing slope of Big Springs Canyon in Tilden Regional Park, Contra Costa County, California (fig. 4). It measures roughly 100 by 500 yards; its long axis runs east and west. There is a gentle slope to the west of approximately 10 to 20 degrees and to the south of 30 degrees. Big Springs Creek drains west along the south border. Rock outcrops and exposures along road cuts and the talus of road fills are

ated with the pineal, have been regarded as parietal-eye rudiments. Hanitsch (1888) reports a parietal eye-like structure in an embryo viper.

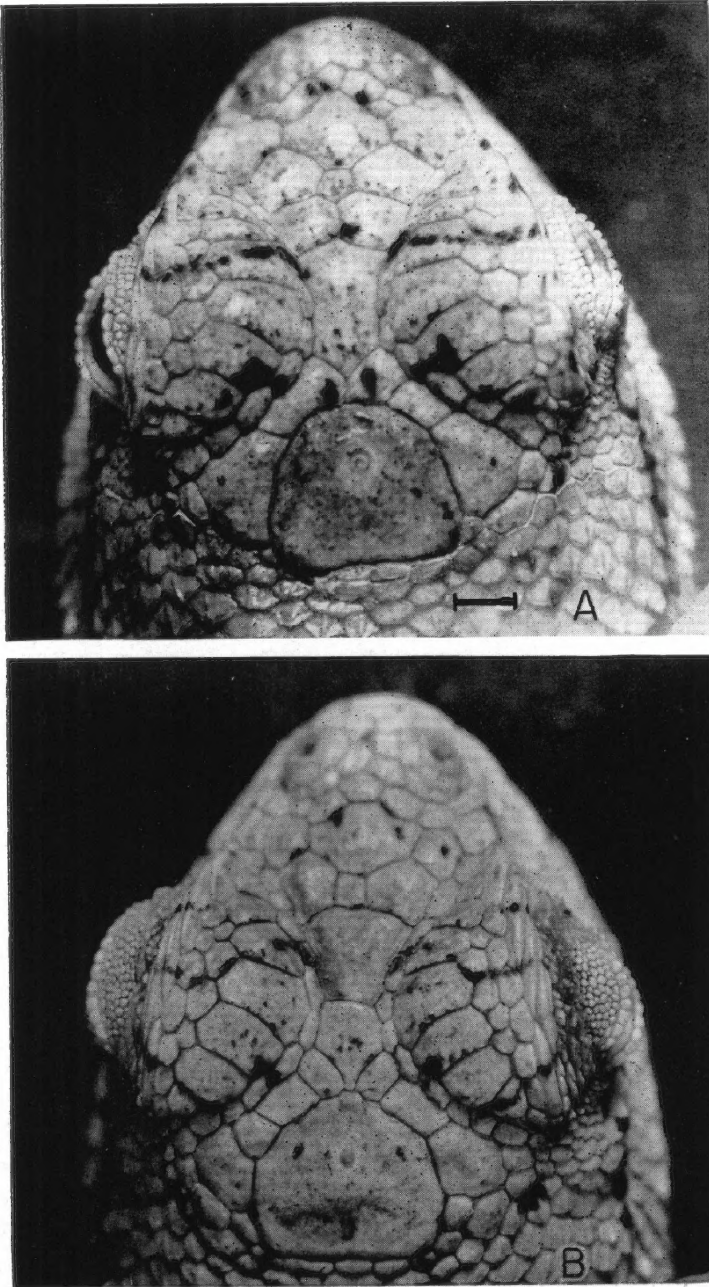


FIG. 3. *Sceloporus occidentalis* two months after surgery, showing complete healing of interparietal scale in sham-operated (A) and parietectomized (B) lizards. Horizontal line in A represents 1 mm.

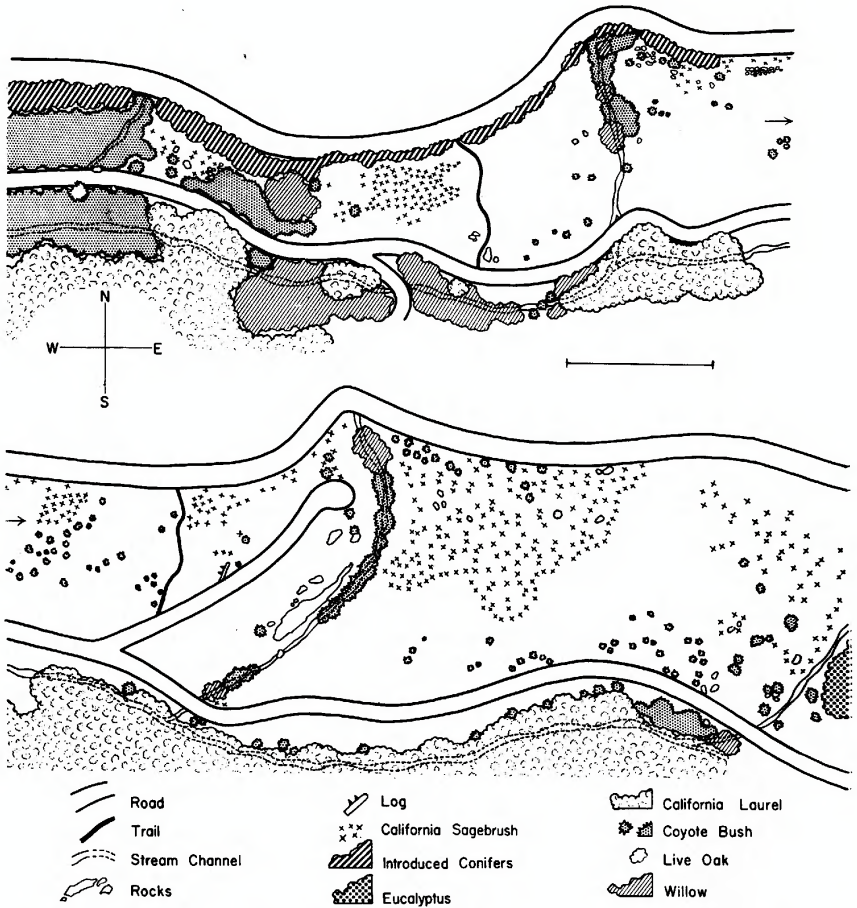


FIG. 4. Aerial view of area in which parietalectomized fence lizards were studied at Big Springs Canyon, Tilden Park, Contra Costa County, California. Lower diagram is continuation of upper one (note arrows). Horizontal line between diagrams represents 50 yards.

focal points of lizard activity. As is characteristic of south-facing slopes in this part of the Coast Range, there are extensive areas of grass (chiefly introduced wild oat) and scattered patches of low-growing brush.

The area was selected to insure maximum returns of surgically treated lizards. Emigration of individuals from the study area was largely limited to the north boundary. Dense vegetation along the south and west boundaries and a eucalyptus grove along the eastern boundary minimized movement of lizards out of the area along these

borders. An unpaved fire road along the north boundary provided us with an effective means of intercepting lizards moving up slope.

All unoperated lizards caught at each visit were brought into the laboratory and divided into two groups, similar as to size range of individuals and sex. All were marked for individual recognition by the removal of toes in varying combinations. No fewer than two toes were removed and no more than three. One group was parietectomized, the other sham-operated, and the animals were returned to their previous locations in the field. Thus at any time there should have been equal opportunity of our seeing the two types, unless parietectomy affected behavior or life expectancy. Subsequent captures of the marked, operated animals were plotted on a map of the area. In addition, the following information was recorded: date and time of capture, size (snout to vent and tail length), sex, coloration, post-surgical appearance of the parietal eye, general physical condition, body temperature at the time of capture, and behavior. Whenever an unmarked lizard was found, it was toe-clipped for future recognition, measured, sexed, treated surgically, and given a field number. An indelible mark was placed on the upper surface of the base of the left hind leg if the animal was parietectomized and at the base of the right hind leg if sham-operated.

We looked for differences in the two types in growth, size of home ranges and movements of individuals, time and frequency of observations, variations in pigmentation, frequency of shedding, body temperature characteristics, and reactions to the observer.

FREQUENCY OF OBSERVATIONS OF SURGICAL TYPES

FIELD ANIMALS: The work began on September 2, 1955, at a time when large numbers of young were available. By September 25, 1956, we had operated on 373 lizards—272 immatures and 101 adults. Of the latter 63 were males (snout-vent 55 mm. or more) and 38 were females (snout-vent 60 mm. or more). On each visit to the study area we recorded the number of parietectomized and sham-operated animals seen or recaptured. In the total scores for the day, each animal was counted only once, even though it may have been seen several times. This method was expected to give us an indication of the relative numbers of the two types exposed above ground. Following the period from September 2 to the end of October, when over half of the animals were marked, the scores on each visit were usually predominantly in favor of the parietectomized lizards, even though the two types had always been introduced into the population in essentially

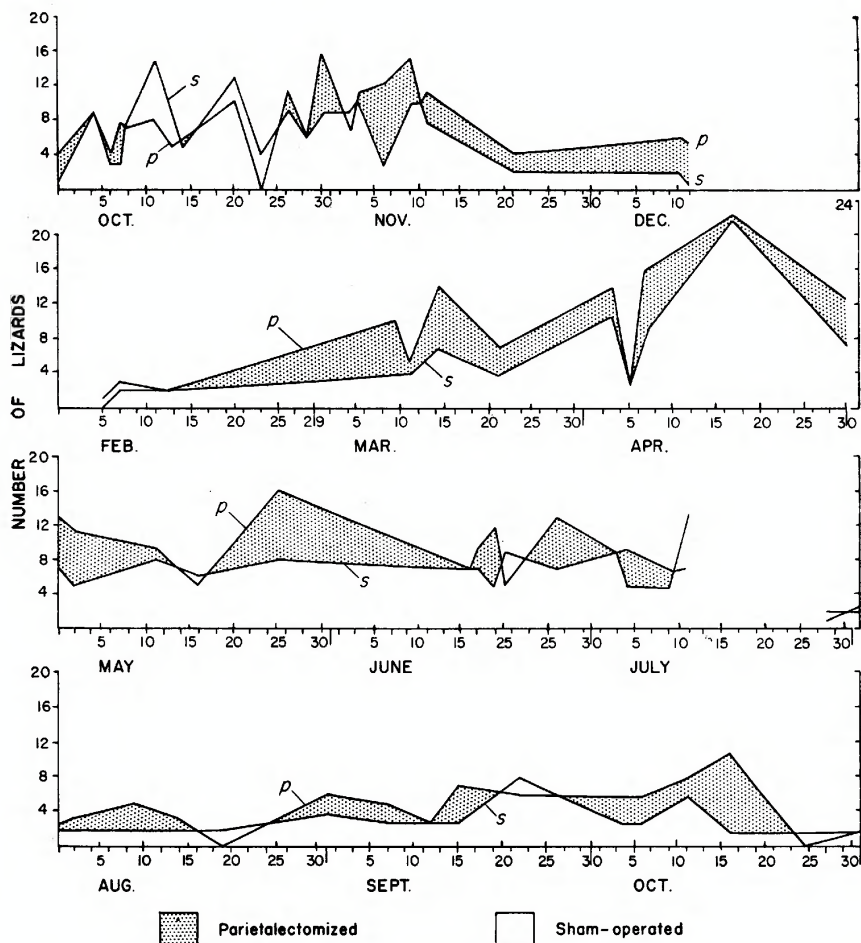


FIG. 5. Number of times parietalectomized and sham-operated *Sceloporus occidentalis* were seen in wild population at Big Springs Canyon near Berkeley, California, from October, 1955, to October, 1956. Each angle in the lines represents a visit to the study area. The two surgical types were introduced into the population in equal numbers, yet the parietalectomized animals were much more frequently seen. Line *p* represents scores made by parietalectomized lizards, line *s* scores made by the controls. Stippled zone indicates times when the scores of the parietalectomized lizards exceeded those of the controls.

equal numbers (figs. 5, 6). On 40 visits the score was in favor of the parietalectomized animals, on 15 in favor of the sham-operated ones, and on eight the scores were equal. From October 23, 1955, to November 4, 1956, surgically treated lizards were seen or caught 703 times,

the parietectomized animals 409 times, the controls 294. The deviation from the expected 50/50 ratio is 4.34 times the standard error¹ and is highly significant. The number of observations made on each surgical type has been calculated as a percentage of the total observations recorded on each visit to the study area (fig. 6). The mean and range in percentage of points made by each type for the total number of visits is as follows:

	MEAN	RANGE	σ	$\sigma \bar{m}$
Parietalectomized	59.5	35.0-84.6	10.94	1.67
Sham-operated	40.4	15.4-65.0		

The difference between the means is eight times its standard error and hence is highly significant. That parietectomy increased the proba-

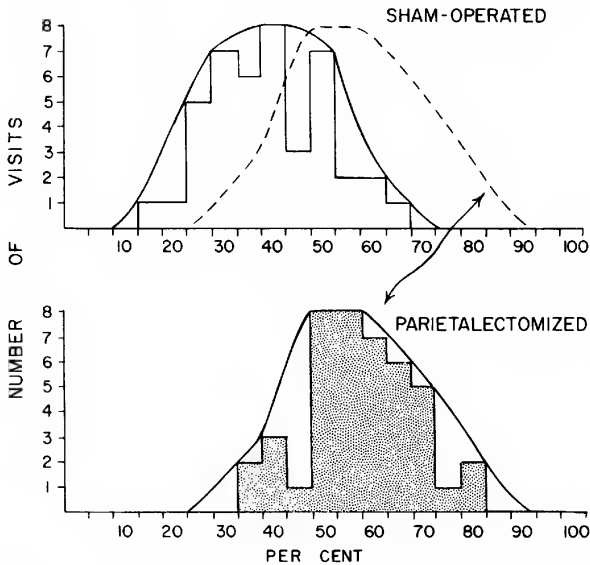


FIG. 6. Percentage of the total score (based on number of observations) recorded on each visit to study area, made by parietectomized and sham-operated *Sceloporus* at Big Springs Canyon near Berkeley. The ordinate indicates the number of visits during which the percentage shown was recorded.

¹ There was no reason *a priori* to anticipate a deviation in one direction in any of the observations made on the two types of lizards. We have used, therefore, a test that takes into account the possibility of deviation in either direction (Neyman, 1950, p. 272). We have used the normal approximation (p. 328) to estimate the probability of obtaining the observed deviation (or greater) by chance alone, whenever the observed numbers are sufficiently large and the probability is not too small. Otherwise we used an exact test (p. 277).

bility of recapture is shown further by the number of individuals of the two types that were never caught again following the first capture. Of 269 young and adults, including essentially equal numbers of the two surgical types, marked from September 2, 1955, through April 3, 1956, 80 (29.7%) were never seen again. Of the latter, 51 (63.7%) were sham-operated, and 29 (36.3%) were parietalectomized. This is a deviation from the expected 50/50 ratio of 2.46 times the standard error of the ratio. The *P* value is 0.01.

Parietalectomized animals were recaptured following the winter period in greater numbers than the controls. Of 193 juvenal individuals marked between September 2 and November 21, 1955 (98 parietalectomized and 95 sham-operated), 81 (41.9%) were recaptured in 1956 after overwintering. Of these 47 (58%) were parietalectomized and 34 (42%) sham-operated. This is a deviation from the expected ratio of approximately 1.4 times the standard error of the ratio and is doubtfully significant. However, the adults, although few in number, show the same type of ratio. Of 38 animals (20 parietalectomized and 18 sham-operated), nine (23.6%) were recaptured after overwintering. Of these, seven (77.7%) were parietalectomized and two (22.3%) sham-operated.

The greatest differences in frequency of observation of the two surgical types occurred in the early morning and afternoon. The parietalectomized animals were nearly twice as likely to be seen as the controls before 10:00 A.M. and about a third again as likely to be seen after 1:00 P.M. During midday the scores were nearly the same (table 1).

It thus can be concluded from the field data on frequency of observations of the two surgical types that parietectomy increases the likelihood of recapture or subsequent observation of these lizards. The

TABLE 1

FREQUENCY OF OBSERVATION OF PARIETALECTOMIZED AND SHAM-OPERATED
Sceloporus occidentalis IN RELATION TO TIME OF DAY
(SEPTEMBER 9, 1955, TO OCTOBER 16, 1956)

Time of Day	Number of Observations ^a		<i>P</i> Values
	Parietalectomized	Sham-operated	
Before 10 A.M.	84 (63.3)	49 (36.8)	0.005
Before 11 A.M.	162 (56.6)	124 (43.4)	0.05
11 A.M. to 1 P.M.	114 (53.3)	100 (46.7)	0.39
1 P.M. to 7 P.M.	201 (58.3)	144 (41.7)	0.004

^aPer cent of total observations given in parentheses.

results suggest that there has been a lowering of the thermal threshold for surface activity, resulting in early emergence in the morning and late retreat in the afternoon, at times of marginal environmental temperatures for activity of fence lizards.

CAPTIVE ANIMALS: Experiments (conducted by Stebbins) with lizards in light-heat gradients in the laboratory and in outdoor cages in Arizona support the field observations and provide additional information on the effects of parietectomy. Tests have been carried out with *Sceloporus occidentalis* from the Berkeley Hills, *Uta stansburiana* from Corral Hollow, Alameda County, and *Uma inornata* from near Garnet, Riverside County, California, and with *Sceloporus undulatus virgatus* in the Chiricahua Mountains, Cochise County, Arizona. Only one of six gradient experiments, involving over 50 lizards, is reported here. In all experiments, a parietectomized group was compared with a sham-operated one as to amount of time spent on the surface of the sand in the runways. In all experiments the parietectomized groups averaged greater exposure than the controls.

In the laboratory at Berkeley the experimental animals were placed in runways that provided a daytime temperature range from about 55° C. at the heated end to 25° C. at the cool end of the cage. These temperatures were well above the upper and lower extremes of the range of body temperature ordinarily found in these lizards when they are active on the surface of the ground in the wild. In most experiments the thermal gradient was maintained by means of an electric light (fig. 7). The floor of the cage was covered with about an inch of coarse sand, in which the animals could bury themselves, and an opaque cover, elevated about $\frac{3}{4}$ inch above the sand, was present at the cool, weakly lighted end. This served as a refuge when the lizards

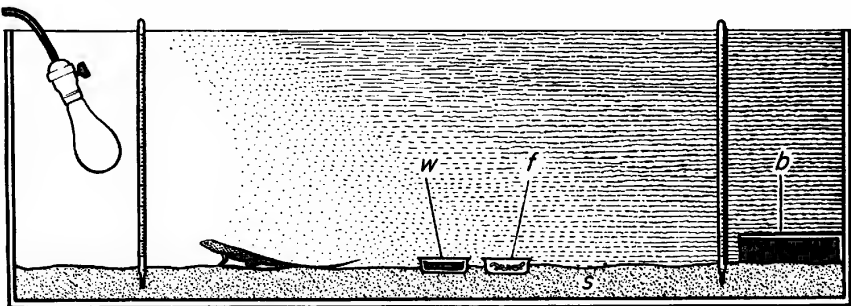


FIG. 7. Photothermal gradient used in studying the behavior of parietectomized lizards. Abbreviations: b, box lid cover; f, food dish; s, substratum of sand; w, water dish.

were on the surface. The locations of the lizards in relation to the light-heat gradient were determined at 20- to 30-minute intervals from about 8:20 A.M. to 5:00 P.M. To make possible recognition of the surgical type, the noses of the animals were marked with indelible pigment, usually red for the parietectomized lizards and green for the sham-operated ones. The location of the color made recognition of a lizard possible when only its head was above the sand. For individual recognition it was necessary to capture the animal and to note the combination of missing toes. In most tests two points were given for each lizard fully exposed on the surface of the sand and one point for each one out of the sand but under the cover or with only the head exposed. Recently we have refined the scoring by giving decreasing points depending upon the distance of the animal from the light. No attempt has been made as yet to separate the effects of visible radiation from those of heat.

On April 5, 1956, 30 juvenal *Sceloporus occidentalis* were selected from a group caught at Big Springs Canyon. They were divided into three groups of 10 individuals each (five males and five females) composed of lizards of similar size. All members of a group received the same colored mark on the nose, red for one group, green for another, and blue for the third. Ten runways were used, with three lizards to a runway and a member of each color group represented in each runway.

The groups were scored on five days from April 6 to 12, 1956, to provide a basis for interpreting postoperative behavior. The lowest scoring group (red) was subsequently parietectomized, the next (green) was sham-operated, and the highest (blue) was used as an unoperated control. The importance of preliminary scoring is shown by this test. The total score for the animals in the blue group was 38.4 per cent greater than that for the red group.

Surgery was performed in the evening of April 12. On April 18 the reds for the first time made a higher score than the greens and from that time until the end of the experiment remained in the lead (fig. 8). The sham-operated and control groups also shifted to a higher level of scoring, the sham-operated animals more so than the controls. The general increase in exposure of all groups probably resulted from increasing familiarity with the runways and adjustment to the presence of the observer. The sham-operated animals may have suffered from an impairment in function of the parietal eye resulting from temporary disturbance of its blood supply following the control operation. These results have been tested by means of the Mann-Whitney rank

test (Mann and Whitney, 1947). The probability that the observed shift in scoring of each group could have resulted from chance is as follows:

GROUP	PROBABILITY	
	AVERAGE	RANGE
Parietalectomized	0.018	0.003-0.075
Sham-operated	0.212	0.003-0.940
Unoperated	0.378	0.011-0.940

Every lizard that was parietalectomized showed marked increase in exposure following surgery; hence the low probability that the shift in scoring of the parietalectomized group could have been due to chance. Although several of the unoperated animals showed a marked increase in exposure, most of the lizards in this group showed little change in over-all behavior throughout the experiment. The sham-operated group occupied an intermediate position in scoring. Before surgery the greens (sham-operated) had totaled 19.5 per cent more points than the reds (parietalectomized). After surgery the reds exceeded the greens by 14.4 per cent. The results of this experiment are in keeping with the field observations.

RESPONSE TO SUNLIGHT

From July 16 to August 29, 1956, Stebbins experimented with lizards in outdoor cages in a more nearly natural environment than had been possible in the laboratory at Berkeley. The work was done at the Southwestern Research Station of the American Museum of Natural History, in the Chiricahua Mountains of southeastern Arizona.

Although the structure and position of the parietal eye strongly suggest that, if functional, the organ responds to radiation (heat and/or light) received from above, our experiments had not yet demonstrated that the stimulus was sunlight. We set out therefore to see if shielding the parietal eye would have an effect similar to removal.

Sceloporus undulatus, abundant about the station, was chosen for study. The animals (all post-breeding adult females of similar size, to minimize effects of aggressive behavior) were confined, eight to 10 to a cage in three outdoor cages, 12 to 15 feet wide (fig. 9).

In cages A and B a metal flange along the upper border of the side of the cage and the supporting posts cast dark shadows, and the screen wire of the sides of the cage a weak shadow. In a metal-sided cage, C, a strip of window screening a foot wide was placed across the top of the cage, on the chicken-wire cover. This provided a weak shadow for

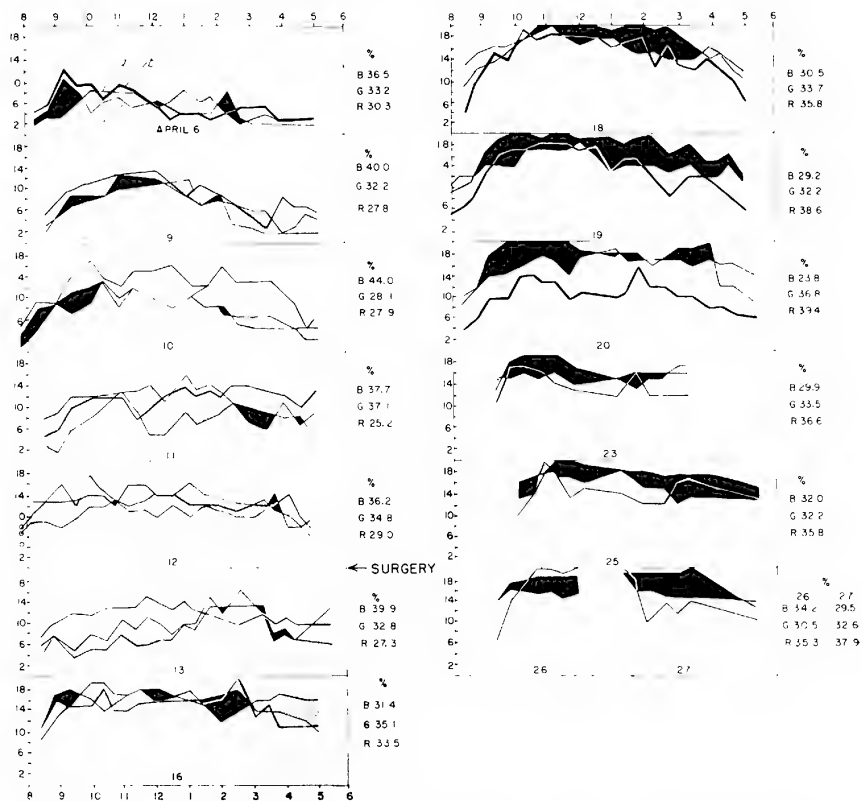


FIG. 8. Daily curves of activity of three groups of juvenile *Sceloporus occidentalis*, based on exposure on the surface of the ground in light-heat gradients. Each group (designated red, green, and blue) consisted of 10 lizards. The red group (r) is shown in black when it scores above the green group; the green (g) group, in stippling when it scores above the red group; and the blue (b) group is represented by a heavy line. The ordinate indicates the number of points made at each observation, shown by angles in the lines in relation to the time of day. Following a period of preliminary scoring, the red group was parietalectomized and the green group sham-operated. Note the subsequent increase in activity of the red group in relation to the green group. The figures at the right of each graph indicate the percentage of points made by each group of the total points made by all the lizards that day.

the lizards in that cage. Artificial burrows and boards provided cover for the lizards. The lizards were scored at 20- to 30-minute intervals from about an hour after sunrise to sunset, nearly every day. They were conspicuously marked with red and green indelible colors, red on the nose, green on the neck for the experimentals and the reverse for the controls. Two colors were used to avoid favoring a color be-

cause it was more readily seen. To measure the amount of exposure to the sun, the lizards were scored as follows:

POINTS	POSITION OF LIZARD
1	Head protruding from burrow or from beneath board cover or lizard fully exposed but in deep shade
2	Fully exposed but in weak shade
3	Exposed in full sunlight

Ten animals were placed in the metal-sided cage C on July 30 at 7:10 A.M. To provide a reference for the interpretation of behavior after experimentation had begun, the animals, half of them temporarily colored red on the nose, the remainder green,¹ were observed until the evening of August 7. On August 7 the two groups had made

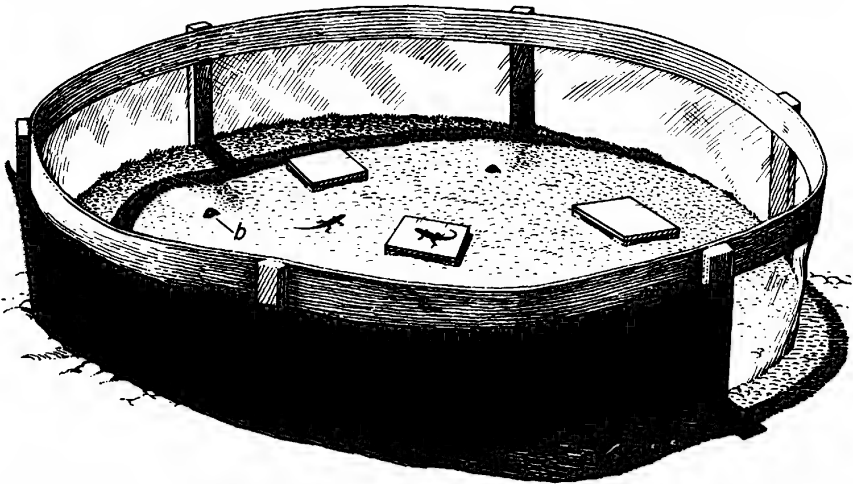


FIG. 9. Field cage B used in the study of *Sceloporus undulatus* in Arizona. Four artificial burrows and five boards, all equally spaced, were provided as cover. Abbreviation: b, mouth of burrow.

almost equal scores (reds 308 and greens 307). On the evening of August 7 the lizards were captured, and a small piece of aluminum foil was inserted through a slit in the rear of the outer horny covering of the interparietal scale and moved into position over the parietal eye of the red group and behind the "eye" of the green group. The identifying colors of the animals were reënforced, and the lizards were returned to the cages the same evening. At 4:50 P.M. on August 14, a week later, the reds (parietal eye covered) had scored 431 points (55.3%), and the greens (parietal eye exposed) 349 (44.7%), an increase of 23.5

¹ Beginning on August 4, the number of animals was reduced to four reds and four greens.

per cent over the greens. This is a deviation from the expected and previously indicated 50/50 ratio of 2.94 times the standard error of the ratio. The P value, with the use of the exact test, is 0.003.

These animals have also been tested as to the amount of exposure on the surface of the ground, with two points allowed for full exposure and one point for exposure of the head only. From August 2 through August 7, 1956, after the groups were reduced to four animals each, the reds made 71 points, the greens 79. After application of the foil the scores were, respectively, 213 and 180. If we may assume that the expected ratio, based on the points made before the foil was applied, was 0.47 to 0.53, the deviation is 2.81 times the standard error of the ratio, with a P value of 0.005, with the use of the approximate test for P . This is in keeping with observations on *S. occidentalis* in the laboratory at Berkeley.

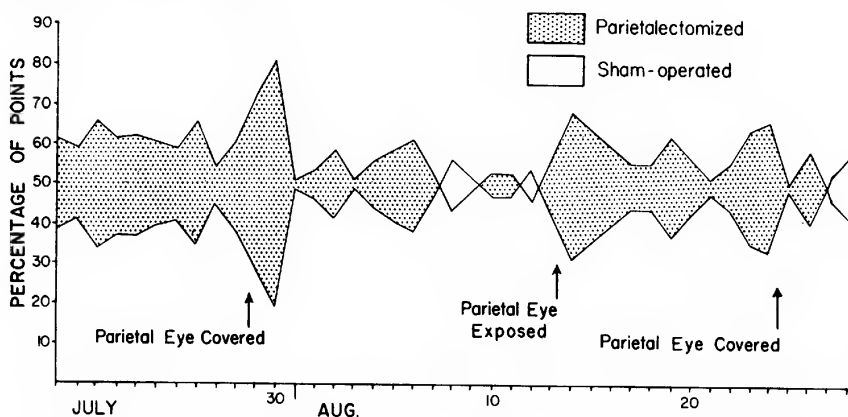


FIG. 10. Changes in activity scores (based on exposure to sunlight) in *Sceloporus undulatus* in outdoor cages. Four parietalectomized and four sham-operated lizards were used. The lower curve of activity is that of the sham-operated group; the upper, that of the parietalectomized group. Angles in the line indicate days on which observations were made. Stippled zone indicates the percentage difference in scoring in favor of the parietalectomized group. Arrows indicate the time at which aluminum paint was placed over and removed from the parietal eye of the sham-operated lizards. Note prompt changes in scoring.

On July 19, 1956, another group of eight animals, four with red on the nose (parietalectomized) and four with green (sham-operated), were placed in cage B. The experiment lasted until August 28. No preliminary check was made on behavior. The two surgical types showed marked differences in scoring, the reds making the higher scores. By 2:24 P.M. on July 28, the reds (parietalectomized) had scored

478 points, the greens (controls) 295, the reds having made 62.0 per cent more points than the greens. The plan in this experiment was alternately to cover and expose the parietal eye of the sham-operated animals to see if this would cause an accompanying change in scores. Aluminum paint was used to cover the "eye." The paint was removed when the "eye" was to be exposed again, by careful scraping with a scalpel. Covering and exposing the "eye" had a prompt and pronounced effect on the scoring of the sham-operated lizards. When the "eye" was covered, their scores closely approximated those of the parietectomized animals and at times exceeded them, but when the paint was removed their exposure was reduced (fig. 10).

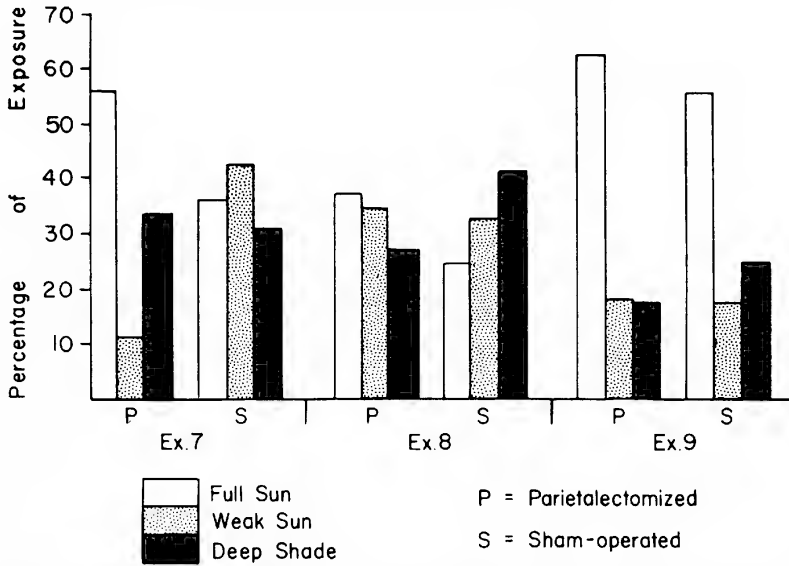


FIG. 11. Differences in exposure to sunlight between parietectomized (P) and sham-operated (S) *Sceloporus undulatus* in outdoor cages in Arizona. Vertical bars indicate the percentage of the total number of observations for each surgical group (P and S) that were made in the sun, weak sun, and deep shade. In each experiment, carried out in separate cages, five parietectomized and five sham-operated lizards were used. Note that in all experiments the parietectomized animals used the sun more than the controls, although differences were slight in experiment 9.

From our observations on *Sceloporus occidentalis* at Berkeley we suspected that, in addition to spending more time on the surface of the ground, the parietectomized lizards were spending more time in full sunlight than the controls. This was found to be true of *S. undulatus* in the outdoor cages (fig. 11).

It seems evident from these experiments that the parietal eye responds to sunlight and that the increased exposure of lizards following parietectomy is due to the absence of the parietal eye and not to some side effect of the surgery.

FRIGHT REACTION

In the field lizards at Berkeley, we found that we could usually predict the surgical type before capture on the basis of behavior. Animals with the parietal eye intact tend to dash for cover quickly and directly, sometimes running 15 or 20 feet. The parietectomized lizards, on the other hand, are less inclined to move, and when they do so they commonly make short dashes of from a few inches to several feet. Moreover they emerge more quickly from cover than do the controls. Laboratory experiments supported the field observations (table 2). Stebbins found that often the parietectomized individuals in the field cages in Arizona moved under a board, only to come out promptly on the other side. They appeared to be markedly phototropic, in keeping with the observations on their greater use of sunlight. The parietectomized lizards behave throughout the day much as normal lizards do when they are basking and have not yet reached the body temperature level for activity (table 4).

The effect of parietectomy on the escape reaction raises questions as to the interpretation of the observations on exposure of lizards in

TABLE 2

INHIBITION OF THE FRIGHT REACTION IN PARIETALECTOMIZED *Sceloporus*

Species	Duration of Observa- tions	No. of Animals ^a	Times Retreated	Per Cent	Times Stayed Out	Per Cent	Total No. of Observations
<i>occidentalis</i>	Jan. 5-6	5P	4	12.5	28	87.5	32
		5S	19	86.4	3	13.6	22
<i>occidentalis</i>	Jan. 7-11	5P	7	26.7	20	73.3	27
		5S	31	70.5	13	29.5	44
<i>occidentalis</i>	Jan. 13-15 ^b	5P	14	50.0	14	50.0	28
		5S	17	70.8	7	29.2	24
<i>undulatus</i>	July 18-23	5P	11	13.0	70	87.0	81
		5S	21	40.0	30	60.0	51
<i>undulatus</i>	July 25-28 ^b	5P	6	7.1	79	92.9	85
		5S	40	40.4	59	59.6	99

^aP, parietectomized; S, sham-operated.

^bSame animals used as in preceding experiment.

the wild population reported above. Can the differences shown have resulted from a greater tendency on the part of the sham-operated lizards to move greater distances when frightened and to tend to remain in hiding? Might the young sham-operated lizards with normal fear reaction have shown, on the average, a greater dispersal tendency than the parietalectomized animals? It would seem that during the period before well-defined home ranges were established, those lizards moving the greatest distances when frightened would most often disperse out of the study area. On the other hand, one must consider the possibility that such a tendency might be counteracted by general activation of those lizards deprived of the parietal eye. Although inspection of the maps of movement seemed to show a slight tendency early in the study for sham-operated animals to make greater shifts in position, this effect (if actually present) was overshadowed by subsequent movements of the parietalectomized lizards. Differences in amount of displacement of the older parietalectomized animals, adult when marked or those that were recaptured six months after reaching adult size, were particularly evident (table 3). We have recorded the recapture points of 1957 in relation to areas of activity determined in

TABLE 3

DISTANCES MOVED^a BY PARIETALECTOMIZED AND SHAM-OPERATED LIZARDS FROM HOME AREAS DETERMINED IN 1955 AND 1956

	No. of Lizards	Distance in Feet Average Displacement	Range	σ	σ_m
Parietalectomized					
Adult when first captured					
Males	4	101	12-216		
Females	5	101	0-438		
Sexes combined	9	101	12-438		
Juveniles ^b and adults combined	25	140	0-711	162.13	32.43
Sham-operated					
Adult when first captured					
Males	8	42	0-66		
Females	3	9	3-18		
Sexes combined	11	33	0-66		
Juveniles ^b and adults combined	20	47	0-240	55.06	12.29

^aBased on recaptures from March 10 to June 22, 1957.

^bLizards that were immature when marked but that reached adult size in the course of the study.

1955 and 1956. The linear distance to the nearest 1955-1956 observation site has been determined for each lizard. It will be evident from table 3 that the parietalectomized lizards have, on the average, shifted about three times as far as the controls. Twelve parietalectomized lizards shifted more than 100 feet, whereas only two controls went beyond this distance. The difference between the means in table 3, with the use of the *t* test, is significant at the 5 per cent level.

We have also obtained an index as to amount of movement of each individual by dividing the average of the distances moved (in feet) between visits by the average time span (in days) between observations. Totaling all observations of the two types we obtained the following result:

	NUMBER OF INDIVIDUALS	AVERAGE	RANGE	σ	$\sigma \bar{m}$
Parietalectomized	27	0.54	0.01-1.29	0.306	0.059
Sham-operated	18	0.45	0.07-0.93	0.293	0.069

The differences shown, although in the direction expected from the observations on the adult lizards, are not statistically significant.

Seemingly greater restlessness of parietalectomized lizards in the laboratory has led to the use of activity chambers to test amount of movement, but these tests are incomplete. It seems clear, however, in view of the field observations that the parietalectomized lizards move about more than the controls. It does not seem likely, then, that losses of control animals from the study area can account for the differences observed. In checking the slope north of the area in the summer of 1957, we found one parietalectomized animal among 25 adults captured. No sham-operated lizards were encountered. This would suggest that there has been little survival of dispersants into this region, as this sample probably represents at least 20 per cent of the total adult population in the bordering area investigated.

With respect to the effect of secretiveness on the scores, it should be mentioned that a lizard in the shadows is probably more likely to be overlooked than one in the sun, and a frightened lizard with a normal fear reaction might be slower to emerge from an underground retreat than one with reduced fear. A continual state of caution might account for late emergence in the morning and for more prompt retreat in the afternoon (at times of marginal temperature conditions) than is observed in the parietalectomized animals. In a wild population the lizards are ever faced with the threat of predation. However, covering the parietal eye with aluminum foil in the Arizona *Sceloporus* had

no effect on the escape reaction, yet it markedly affected basking behavior. Many of the lizards in the cages at Berkeley were under observation for such long periods that they became somewhat tame, yet differences in scoring between the two types occurred over many months.

Differences in the escape reaction no doubt contributed somewhat to the results reported on frequency of observation of the two types in the field population. It also seems certain that increase in both mobility and exposure on the surface of the ground and to the sun was important.

LIFE EXPECTANCY

Under conditions in the field the behavior of the parietalectomized lizards, quite apart from what it may reflect as to their physiological condition, in itself would seem to make certain a more rapid decline in their numbers than the controls. Exposure in well-illuminated areas combined with reduction of the tendency to seek cover in the presence of a potential enemy would seem to make them more vulnerable to predation.

For some time we expected a shift in the ratio from that favoring the parietalectomized lizards to one favoring the sham-operated ones. This shift did not occur in over a year and a half of observations. From March 10 to June 14, 1957, the number of observations of the two types was still in favor of the parietalectomized animals (52 observations of parietalectomized lizards to 30 observations of controls). This is a deviation from the expected 50/50 ratio of 2.43 times the standard error of the ratio. The *P* value is 0.02.

There may now actually be fewer parietalectomized lizards in the area of study than controls, but their greater exposure and reduced tendency to retreat more than make up for their smaller numbers.

There are indications that the parietalectomized lizards are at a disadvantage not only in behavior but also in vitality. Of 12 animals (six parietalectomized, six sham-operated) representing three species, Stebbins found that, with the exception of one individual, all the parietalectomized animals died before the controls when deprived of food. This would be expected with increased exposure to body temperature levels of 32° to 38° C. (those sought during surface activity) and with increased locomotory activity. Differences were not evident in survival rate in the recovery period following surgery; hence the reduced vitality would not seem to be due to differences in the surgery apart from destruction of the parietal eye. Long-term survival seems to be affected, however, when food is reduced or eliminated.

The greater use of heat and the increased activity of the parietal-ectomized lizards suggest the possibility that, owing to metabolic excesses, parietectomy may shorten the life span and that the parietal eye may play a part in regulating the intensity and hence the duration of the life of the individual (see Selye, 1946, 1956).

THERMOREGULATION

It has become evident in recent years, chiefly as a result of the studies of Cowles and Bogert (1944), Bogert (1949), and others, that many reptiles, far from being at the mercy of their thermal environment, do in fact maintain their body temperatures at fairly constant levels when environmental temperatures are sufficiently high to permit them to do so. In a heliotherm such as *Sceloporus occidentalis*, after the thermal threshold for activity is reached by basking, the body temperature is maintained by orientation of the body in relation to the sun and movement to and from warm and cool areas within the habitat until falling temperatures cause the animal to seek shelter. Variation may be only a few degrees Centigrade (from 32° to 38° C.) throughout the active period. During this period such a reptile may be regarded as approximating the thermal state of a warm-blooded animal, and the thermoregulatory behavior that occurs indicates a marked degree of temperature discrimination.

A prompt heat-avoiding reaction is essential in those species that operate at levels only a few degrees below their maximal temperature tolerance. In *S. occidentalis* the upper limit of voluntary tolerance is 40° to 41° C. and is only 3° to 5° below the temperature at which loss of coordination and paralysis from heat may occur (44°–45° C.). Small species (and the young of larger forms) that are active at body temperatures near their critical maximum must be particularly reactive to high temperatures because of the rapidity with which they absorb heat.

We have considered the possibility that the parietal eye is a thermoreceptor important in thermoregulatory behavior. Rabl-Rückard (1886), long before the concept of a narrow "optimum" temperature range for reptilian activity was recognized, suggested that the "eye" might provide those reptiles that possessed it with a more delicate means of detecting differences of temperature than existed anywhere else in the body. No one, however, has shown that it so functions (Stebbins, 1944). Many previous workers, influenced by the resemblance of the organ to the lateral eyes, have speculated that it is a visual receptor. This, along with the frequent reference to the organ as vestigial,

and the fact that many species lack a parietal eye nerve have no doubt tended to deter exploration of the possibility of temperature detection.

In *Sceloporus* and many other lizards we have studied, the structure of the "eye" suggests that it may be a thermoreceptor. The cornea is yellow and perhaps serves to filter out shorter wave lengths. The retina is heavily impregnated with melanin and is backed by a reflective guanin tapetum, reminding one of a black plate collector used in solar heat-trapping devices.

Although our study is incomplete, we can report some facts at this time. Removal of the "eye" has so far resulted in no well-defined differences in cloacal temperature readings in lizards that were exposed on the surface of the ground in the field study area (table 4) and in the photothermal gradients in the laboratory. Evidently during the active period the ability of the parietectomized lizards to stay within the range of body temperature for normal activity is good. However, these data do not eliminate the possibility that parietectomized lizards may differ from the controls in other aspects of their thermal reactions. Their tendency towards early emergence in the morning suggests the possibility that they are activated at lower thermal levels.

TABLE 4

BODY TEMPERATURES (IN DEGREES CENTIGRADE) OF *Sceloporus occidentalis* AT BIG SPRINGS CANYON, SEPTEMBER 9, 1955, TO JUNE 7, 1957

	Number of Readings	Average	Range
Parietalectomized	40	34.1°	28.0–37.5°
Sham-operated	30	34.7	32.0–39.5
Unoperated	57	34.8	31.4–37.9

Under conditions of captivity, there has been an indication that the parietectomized lizards may press the upper limits of voluntary temperature tolerance more than do the controls, but there has been no confirmation of this in the field. Stebbins found that of a total of 108 cloacal temperatures taken in caged animals, those lizards with the parietal eye covered with aluminum paint had body temperatures above 37.5° C. more often (7.3%) than the controls.

Up to this point we refer to thermoregulation in the sense of adjustments that may be made, minute by minute, as a reptile moves about in the thermal mosaic of its habitat. We must also consider temperature regulation in another sense. What is the optimum amount of exposure

to the thermal levels of the "normal activity range"? There must be undesirable extremes—too little or too much time spent at the levels for "normal activity." Such an optimum would depend on the species and would be expected to vary individually with heredity, age, sex, stage of the reproductive cycle, season, and so forth. Perhaps the parietal eye functions in relation to this longer-term thermoregulation.

We point out above differences in amount of exposure on the surface of the ground and to sunlight in both field and caged lizards. As we have found that the body temperatures of lizards buried in the ground or under rocks, logs, and other cover average significantly lower than those of lizards on the surface, it can be concluded that, on the average, the parietectomized lizards spend longer periods of time at the thermal levels of "normal activity" (32° – 38° C.) than do the controls.

CHARACTERISTICS UNAFFECTED BY PARIETALECTOMY

We found no differences in rate of growth (fig. 12), although reports in the literature on mammals had led us to consider the possibility of such an effect. Our data on the rate of shedding and pigmentation are inconclusive but suggest that parietectomy has little or no effect.

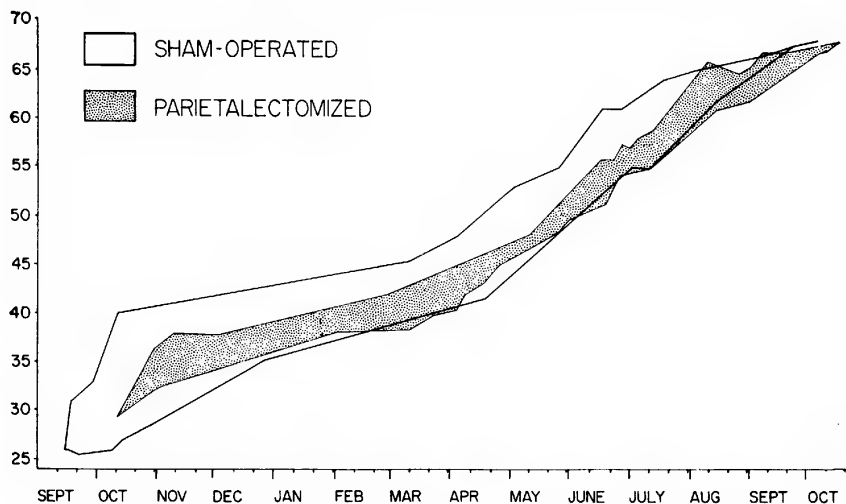


FIG. 12. Growth rates of *Sceloporus occidentalis* in a wild population at Big Springs Canyon near Berkeley. The stippled and unshaded areas contain the growth curves of five parietectomized and five sham-operated animals studied during the period September 15, 1955, to October 16, 1956, when adult size had been reached. These growth curves are representative of the growth of 21 parietectomized and 19 sham-operated animals followed over a period of six months or longer. Measurements are of snout to vent length in millimeters.

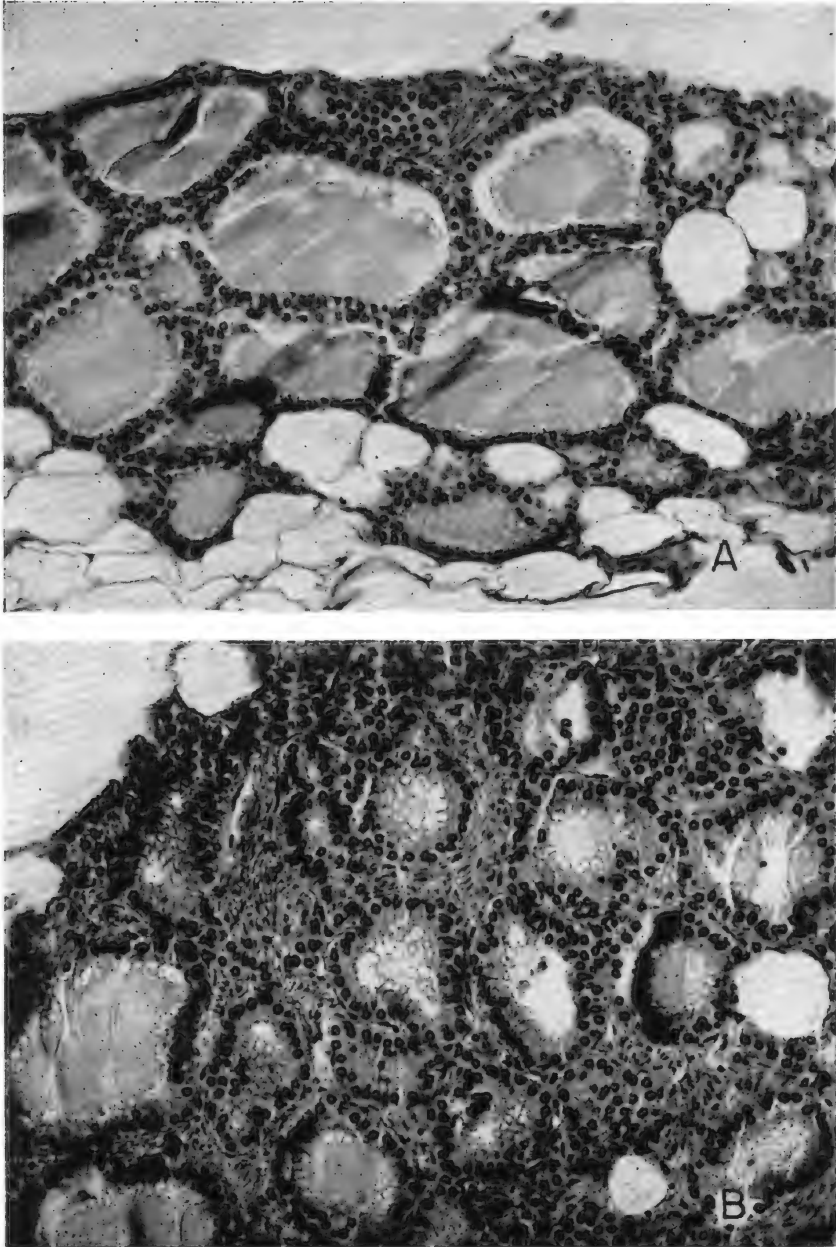


FIG. 13. Photomicrographs of thyroid gland follicles of adult sand lizards, *Uma inornata*. A Sham-operated lizard. B. Parietalectomized lizard, six months after surgery. $\times 225$.

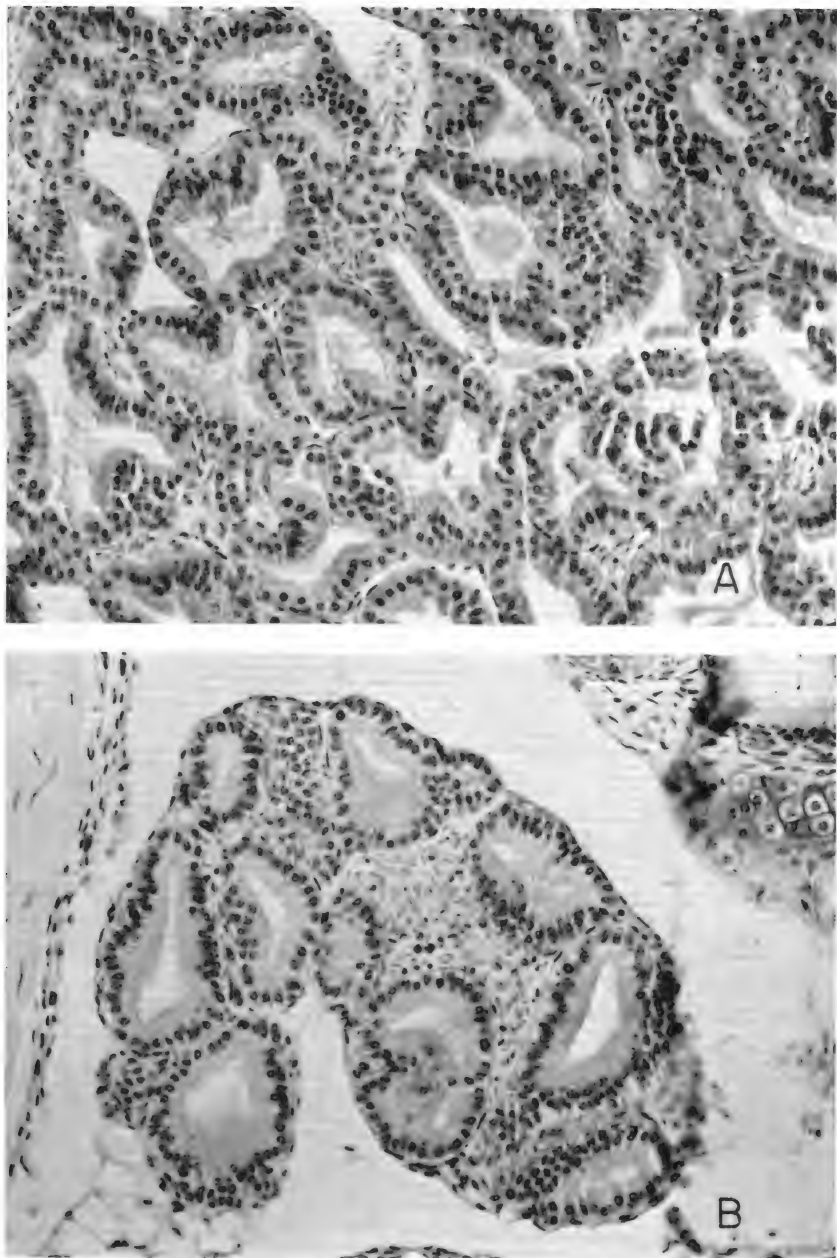


FIG. 14. Photomicrographs of the thyroid gland. A. Parietalectomized adult male sand lizard (*Uma inornata*) eight months after surgery. $\times 225$. B. Fence lizard (*Sceloporous occidentalis*) nine months after parietectomy. $\times 225$.

THE THYROID GLAND

Both authors, Eakin particularly, have investigated the thyroid gland in laboratory and field lizards on the theory that the increased amount of time spent on the surface of the ground and the increased exposure to radiation of the parietectomized animals might be related to increased thyroid activity. The results to date show a greater tendency for the parietectomized lizards to display a heightened thyroid epithelium and a reduction or loss of colloid than the sham-operated animals.

In an experiment with adult sand lizards (*Uma inornata*), all animals were kept for six months in light-heat gradients (see pp. 13-14). All sham-operated lizards (two males and three females) had a lower thyroid epithelium than the parietectomized lizards (two males and three females). There was, however, a gradation in epithelial height between the two groups. Figure 13 shows the extremes in epithelial height after six months of exposure in the gradients. Figure 14A depicts the condition of a parietectomized individual eight months after surgery. Note the marked hypertrophy of the epithelium and loss of colloid.

Our results parallel those of Pflugfelder (1956) who found thyroid hypertrophy following epiphysectomy in the guppy (*Lebistes reticulatus*). A fuller report on the effects of parietectomy on the thyroid will be made later.

DISCUSSION

The parietal eye in the lizards studied has been shown to be involved in the regulation of exposure to sunlight and the amount of time spent on the surface of the ground. The increased exposure following removal or impairment of the "eye" suggests that it functions in the inhibition of activity levels that are directly dependent on solar radiation. Withdrawal from the sun and retreat underground are usually accompanied by a reduction in body temperature and locomotory activity. Heart and respiratory rate (metabolism) are reduced. It is of particular significance that, by influencing behavior, the parietal eye can affect these vital processes at a time when the environment would allow continued high-level activity.

How does the parietal eye produce its effect? In *Sceloporus*, in the absence of a parietal-eye nerve, it appears probable that the organ is secretory. Globes of what appears to be a secretory material (stained pink with haematoxylin-eosin) protrude from the ends of the rod-like cells of the parietal-eye retina in sections of the "eye" of the lizard

Xantusia vigilis. Strands of coagulated material in *Sceloporus* extend from the retina into the chamber of the "eye." Secretory material probably accumulates in the chamber of the "eye" and passes out through the walls of the organ into the surrounding capillary network. Blood from the "eye" passes posteriorly in a small vein which joins the posterior cerebral vein near the distal end of the epiphysis. For histological details of parietal eye structure in iguanid lizards, see Ritter (1890) and Stebbins (1944).

The zenithal "eye," lacking lids and an iris mechanism and hence having little capability of modifying the radiation received by the retina, continually obtains a representative sample of sunlight reaching the skin of the dorsal surfaces of the body. This is not true of the lateral eyes. Much of the radiation they receive is reflected and degraded in intensity. They view a lateral and much more variable field. Probably there is little carry-over of parietal-eye secretion from periods of bright illumination because of the small size of the secretory layer and the limited storage capacity of the chamber of the "eye." Thus the flow of secretion to the blood would cease or be reduced quickly after exposure. If the parietal eye were large, with many secretory cells and a large cavity, a greater lag could be expected in the rise and decline of the blood concentration of the parietal-eye hormone.

Our observations suggest that inhibition is intermittent, and whether it will occur or not and the intensity of its effect at any particular time may be assumed to depend on many variables—weather, heredity, age, sex, physical vigor, amount of previous activity and photothermal exposure, stage in the sexual cycle, and state of nutrition.

When warm weather in the field follows a period of reduced sunlight or when the lights are turned on in the runways in the laboratory after several days of darkness, differences in the scoring of parietalectomized and sham-operated lizards tend to be reduced. The control animals, having experienced reduced parietal-eye stimulation during the period of reduced heat and light, then behave more nearly like the parietalectomized lizards. Conversely, when periods of prolonged and intense light and heat are followed by reduced illumination, marked differences in scores, at least during the beginning of the mild period, are likely to result. Evidently parietal-eye stimulation during the period of intense illumination causes inhibition of the controls, when photothermal conditions become marginal for activity.

We observed some parietalectomized animals in our experiments that seldom exposed themselves. In such instances temperament, state of nutrition and vigor, and inhibiting mechanisms other than the pineal

system may override the permissive high-level activity afforded by damage to the parietal eye. A diurnal terrestrial ectotherm must be exposed to solar radiation to initiate and maintain high-level activity. Thus, if some factor other than the parietal eye hormone is inhibitory, the exposure required to bring about metabolic excesses does not occur, and the "eye" is not called into play. Furthermore, a lizard under stimulation, such as one at a high level of sexual activity, although having an intact pineal system, may be more active than a sexually immature or senile animal with the parietal eye damaged. It seems that variable results should be expected.

Species differences, small samples, lack of study of behavior effects, surgical damage to other structures, age and sex differences, timing with respect to cyclic phenomena, and many other variables that can shift the inhibitory-stimulatory interaction in one way or another account we think, in part at least, for the partly inconsistent results in pineal experimentation.

THEORY OF PINEAL FUNCTION

The pineal-epithalamic system in the roof of the third ventricle and the pituitary-hypothalamic complex on its floor display certain parallels in structure (Stanley-Jones, 1956). Chiefly on the basis of histological evidence Roussy and Mosinger (1938) developed a theory of a "*système hypothalamo-hypophysaire*" as opposed to a "*système epithalamo-épiphytaire*." The hollow of the pineal recess corresponds with the hollow of the infundibulum, the glandular part of the epiphyseal evagination with the neurohypophysis, and the correlation centers of the habenulae correspond with the hypothalamic centers. Fiber tracts in the walls of the diencephalon connect the two systems. When ectotherms (Cowles, 1940) are included, it can be said that photoreceptors may be associated with both regions. There is evidence that in some endotherms fibers from the optic tracts enter the hypothalamus, placing the lateral eyes in communication with the autonomic nervous system and pituitary gland; in ectotherms the median-eye nerve carries fibers to the habenulae. In ectotherms, in the absence of an eye-like vesicle, transparency of the skull roof may permit the epiphysis itself to receive solar radiation (Breder and Rasquin, 1950).

There is some experimental evidence to suggest an antagonistic relationship between the pineal apparatus and the pituitary (Kitay and Altschule, 1954, pp. 103-104) and to indicate that the action of these glands, at least in some vertebrates, can be influenced by changes in solar radiation (light and/or heat). The lateral eyes are known to

be involved in gonadal recrudescence, via the hypothalamus and pituitary (mammals, birds). Young (1935) and Pflugfelder (1956, 1957) have obtained in the lamprey and the fish *Lebistes*, respectively, pineal activation by light and highly suggestive evidence of an inhibitory effect of the pineal on the pituitary. Removal of the median eye is followed by increased activity and exposure to sunlight in heliothermic lizards, and hence the parietal eye may be inferred to have an inhibitory function. The concept of an antagonistic relationship between the activity of the pineal body and the anterior lobe of the pituitary was suggested long ago by Berblinger (1926) and Calvet (1934) and has been reaffirmed by others, lately by Engel and Bergmann (1952), Lowenstein (1952), Thiéblot and Le Bars (1955), and Pflugfelder (1957). However, it should be pointed out that there is considerable negative evidence with respect to pineal-pituitary interaction.

In lizards the parietal eye (associated in development with the epiphyseal anlage) plays a part in helping to prevent metabolic excesses and in the reestablishment of homeostasis following periods of increased activity. It appears that it should be aligned with those mechanisms concerned with the inhibitory-restoratory and anabolic functions of the body. Whether or not the pituitary gland is involved has not been determined. Possibly the pineal mechanism operates through hypothalamic centers which in turn may influence pituitary function, or there may be a direct effect on appropriate end organs. Lowenstein (1952) has suggested that the pineal reinforces activity of the sympathetic nervous system. Our results do not seem to support this conclusion. The zenithal location of the pineal apparatus places it in a position to register changes in solar radiation, on which the rhythm of activity in cold-blooded animals chiefly depends. The median eye is not a visual receptor in the usual sense but rather seems to register the amount of radiation received. Inhibition could insure the maintenance of energy reserves and help provide a margin of safety for emergency situations. It may prevent a rapid spending of adaptation energy (Selye, 1956) in excessive activity.

If this theory is correct, what now may be the role of the pineal in warm-blooded animals? Camp (Camp and Welles, 1956) has pointed out that the reduction of the parietal foramen in cynodont reptiles and its absence in bauriamorphs and "ictidosaur" may indicate that the need for a parietal "eye," so well developed in contemporary dicynodonts, was waning in the Triassic "reptilian" ancestors of the mammals. Other skeletal changes suggest that internal control of body temperature had developed (Brink, 1956). In the advanced mammal-

like reptiles, then, the median eye may have disappeared in conjunction with the development of a constant internal thermal environment.

The nerves and nerve tracts associated with the pineal in ectotherms and endotherms, and the absence in endotherms of specializations in the cranial roof for the reception of solar radiation, suggest that there has been a shift in the relative importance of external and internal stimuli in pineal activation. In reptiles with a median eye and nerve, for example, fibers from the "eye" course towards the brain, and fibers of the pineal tract, arising from cells in the wall of the epiphysis, extend to the posterior commissure (Gladstone and Wakely, 1940, p. 246). In mammals, however, when nerve fibers are present in the base of the pineal, they seem to extend from the brain to the gland, and in adult birds no nerve connection exists (*op. cit.*, p. 291). Thus Gladstone and Wakely (1940, p. 409) state that ". . . nerve-fibers which originally carried impulses from the receptive organs of the pineal system to ganglia of the central nervous system have been either wholly or partially supplanted by nerves which are afferent to the epiphysis." It would appear that in endotherms the pineal responds mainly to internal stimuli carried in nerves or transported in the blood. Activity itself (especially high-level activity) may bring about pineal activation which in turn contributes to the restoration of homeostasis.

Although research on the pineal of mammals is inconclusive and controversial, certain of the results that are available tend to support the view that the organ has an inhibitory effect on a number of bodily functions (see Kitay and Altschule, 1954). Pineal tumors in man, involving the stroma of the gland and resulting in restriction of the secretory parenchyma, are correlated with hypergonadism, and there is evidence for increased activity of the reproductive system following pinealectomy in experimental animals. The effect of pinealectomy on the thyroid and pituitary glands of various mammals has been reported as hypertrophy, hyperplasia, or no effect. Changes in blood chemistry following pinealectomy in rabbits and injection of pineal extract in humans suggest an influence on body metabolism, particularly the metabolic actions of the adrenocortical hormones (Kitay and Altschule, 1954, p. 103). Pineal extracts have been used to lower high blood pressure in man (Engel and Bergmann, 1952) and in the treatment of sexual hyperexcitability in domestic animals (Hutschenreiter, 1948). The lowering of blood pressure in the rat, following the injection of pineal extract, has been used by Bergmann (1955) as a test of extract potency.

The effect of damage to the pineal system in lizards, namely, the

thyroid changes and the general increase in activity, seems in accord with certain of the effects of pinealectomy reported in mammals. We have not yet studied possible effects on the reproductive system. Although the effect of pineal secretion on blood pressure in man has yet to be well documented, Engel and Bergmann's (1952) clinical observations seem reasonable in view of our observations on lizards. It may be assumed that when a lizard withdraws from the sun, retires to a cool location, and reduces activity, its heart rate and blood pressure fall. The parietal eye has been shown to influence such withdrawal behavior. May there have been a carry-over of a hemodynamic function in reptiles to their mammalian descendants?

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SUMMARY

The function of the parietal eye in four species of western North American lizards was investigated by surgical removal of the "eye" (parietalectomy) and by covering the "eye" with aluminum foil. The species studied were *Sceloporus occidentalis*, *S. undulatus*, *Uta stansburiana*, and *Uma inornata*; the first two species were investigated most intensively. A population of *Sceloporus occidentalis* in Berkeley Hills, California, was studied from September, 1955, to June, 1957. Marked parietalectomized and sham-operated individuals were returned to the field to original points of capture, and their subsequent behavior was observed. The two surgical types were always introduced in equal numbers. Other lizards were studied in photothermal gradients in the laboratory. The following results were obtained:

1. Individuals of all four species increased their exposure to sunlight (or artificial light in the laboratory) following removal of the parietal eye. There was prolongation of the time spent exposed on the surface of the ground and greater use of high-intensity illumination.

2. Although these lizards are heliotherms, depending directly on the sun for elevation of their body temperature to desired levels, no differences were found between the parietalectomized and control lizards in body temperatures recorded during the period of surface activity. Both in the field and laboratory, however, the parietalectomized lizards extended the length of time spent at the thermal levels of "normal activity."

3. The increased exposure to sunlight following parietalectomy is accompanied by increased locomotory activity, as judged by the restive behavior of captives and the shifts in position of surgically treated lizards released in the field. The parietalectomized animals average three times greater displacement from previously determined home ranges than the sham-operated animals.

4. The parietalectomized lizards were less inclined to retreat upon

the approach of the observer than were the sham-operated ones. The pronounced heliothermism perhaps works antagonistically to the normal retreat reaction.

5. The thyroid gland of parietalectomized lizards tended to show hypertrophy and loss of colloid, which suggests that there is a relationship between thyroid activity and the behavioral changes observed.

6. That sunlight is the stimulus to the parietal eye seems indicated by the increased heliothermism that occurred following the use of aluminum foil shields over the "eye." In experiments with foil, the parietal eye was left intact.

7. Parietalectomized lizards deprived of food appeared to be less viable than sham-operated lizards. Increased metabolism probably resulted in more rapid exhaustion of their energy reserves. Additional work is, however, required before this point can be fully documented.

8. Microsections of the parietal eye of *Sceloporus* failed to reveal any nerve connection between the "eye" and the brain. The retina of the "eye" appears to be secretory, and its activity probably fluctuates with the intensity of solar radiation to which the eye is exposed.

It may be concluded that the parietal eye in the diurnal lizards studied functions in helping to regulate the amount of exposure to sunlight. After a period of exposure, the length of time probably varying with changes in the duration and intensity of sunlight and the physiological condition of the animal, inhibition to activity begins. Because exposure to sunlight is required to maintain normal activity levels, parietal-eye inhibition may function to prevent metabolic excesses and to insure the maintenance of energy reserves. The "eye" thus may influence the intensity and perhaps also the duration of the life of the individual.

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